Rev. Écol. Biol. Sol, 1975, **12** (2): 449-457.

Interspecific and seasonal analyses of the gut contents of three Collembola (Family Onychiuridae)

BY

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INTRODUCTION

In a square metre of most soils, several hundred species of arthropods may be found. Amongst these arthropods, Collembola, which generally attain populations of several thousand individuals per square metre are preponderant.

Despite numerous studies, the biotic relationships, and especially trophic interrelationships, of Collembola are still little understood. Almost nothing is known of their digestive physiology; their processes of food selection; or the real diet of most species. Recent studies by KNIGHT and ANGEL (1967), BÖDVARSSON (1970), GILMORE and RAFFENSPERGER (1970), and McMILLAN and HEALEY (1971) indicate that the gut content of a single species taken from several habitats may show greater diversity than the gut contents of several species taken from the same habitat. This would suggest that Collembola are indiscriminate feeders. However, general ecological theory suggests, in the principle of competitive exclusion, that species cannot coexist while sharing the same food resources (DEBACH, 1966; SLOBODKIN, SMITH and HAIRSTON, 1967).

This paper describes the qualitative and quantitative composition of the gut contents of three species of the family Onychiuridae during a 12-month study.

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MATERIALS AND METHODS

1. Animal materials.

Individuals of *Onychiurus armatus* (Tulb.) Gisin, *Onychiurus furcifer* (Börner) Gisin and *Tullbergia callypygos* Börner, were collected at monthly intervals between December 1969 and November 1970 from soil taken from the periphery of a nest of *Formica rufa L.* (a woodland ant). The nest was located in a mixed coppice of sweet chestnut (*Castania sativa* Mill.) and beech (*Fagus sylvatica* L.) in Blean Woods National Nature Reserve, near Canterbury in south-east England. The soil in the periphery of the nest was a mull-like moder humus form. A partial cover of debris is present over the nest during summer as a result of the ants nest building activities and a complete leaf litter cover is present during autumn and early winter as a consequence of leaf fall.

On each sampling occasion a random block fo soil 100 mm × 100 mm and 50 mm deep was dug, within a reference grid, from the ant nest. In the laboratory, Collembola were extracted alive from the soil using a Tullgren type funnel. Five adults of each species, with a visibly full gut, were selected for gut analysis.

As an experimental control, and also to ascertain the possible composition of gut components in a hypothetical animal, artificial guts, comparable in length and volume to that of an average adult Onychiuridae, were drawn from fine capillary tubing. On each sampling occasion five artificial guts were filled by pushing each tube, at random, into the sample of soil from which animals for gut analysis were later to be extracted.

2. Separation of gut contents.

The gut contents of individual Collembola was obtained using the technique described by McMILLAN and HEALEY (1971). The technique involves the precipitation of dispersed gut content particles, of a Collembola, onto gridmarked Millipore filters. The filters are individually mounted between slide and coverslip in Canada Balsam and examined under oil immersion and phase contrast at a magnification of 1250X.

3. Analysis of gut contents.

The following materials were categorised, and counted:

(i) Plant material
- particles < 10 µm
- particles 10-20 µm
- particles > 20 µm

(ii) Fungal material
- hyphae diameter < 2 µm
- hyphae diameter > 2 µm
- spore, aseptate
- spore, septate

(iii) Pollen grains

(iv) Enchytraeid chaetae

(v) Other animal remains

(vi) Mineral particles

RESULTS

The major components of the gut in each 'species' were plant, mineral, and fungal material (Fig. 1). Pollen, enchytraeid chaetae, and other animal remains each accounted for less than 0.5 % of the gut content. Enchytraeid

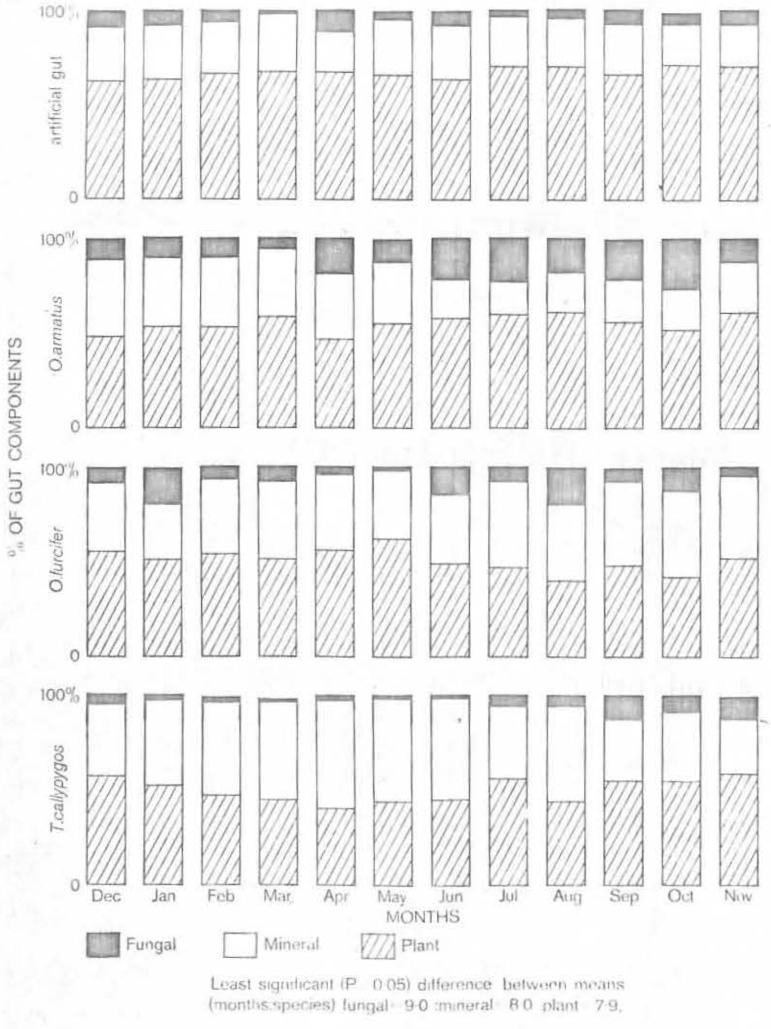

FIG. 1. — Monthly mean (N = 5) percentage of major gut components (plant, mineral, fungal) in three Onychiuridae and an artificial gut.

chaetae were not found in *T. callypygos* and other animal remains were present only in the artificial gut. The three arbitrary size categories of plant material had a similar order of abundance in each 'species'. Particles, less

than 10 μm, were most abundant (35 - 62 % of total gut content) and particles greater than 20 μm (less than 2 % of total gut content) were least abundant. In each 'species' most of the particles of plant material were apparently in an advanced state of decomposition, because the fragments were dark brown, and recognisable cell structures were uncommon.

The ingested fungal components were mostly hyphae (spores comprised only 3 - 6 % of fungal material in each 'species'). In general, hyphae less than 2 μm in diameter were 140 - 380 μm in length and hyphae greater than 2 μm in diameter were 4 - 50 μm in length. In *O. armatus* and *T. callypygos* hyphae of small diameter were most numerous, whereas in *O. furcifer*, and artificial gut, hyphae of large diameter were more abundant. Aseptate spores were more common than septate spores in all 'species'.

Analysis of variance between plant, mineral, and fungal gut components and the four 'species' (Table I) show significant ($P < 0.001$ or $P < 0.01$) differences between 'species'; months; and 'species' x months.

TABLE I

Analysis of variance between four 'species' of Onychiuridae and the mean (N = 5) percentage of three major gut components

Gut Component	Source	Sum Sq.	D.F.	Mean Sq.	F. Ratio
1. Plant	Species	10,595	3	3,531	88.0 ***
	Months	1,004	11	91	2.2 **
	Species × months	4,863	33	147	3.6 ***
	Error	7,628	186	41	
2. Fungal	Species	4,183	3	1,394	42.6 ***
	Months	1,733	11	158	4.8 ***
	Species × Months	3,413	33	103	3.1 ***
	Error	6,150	186	33	
3. Mineral	Species	14,144	3	4,714	104.0 ***
	Months	2,336	11	212	4.7 ***
	Species × Month	7,984	33	242	5.3 ***
	Error	8,341	186	45	

Significance *** $P < 0.001$.
** $P < 0.01$.

To detect significant ($P = 0.05$) differences, in the percentage of plant fungal, and mineral components, between individual 'species' and months the least significant difference between means was calculated (Fig. 1). Significant ($P = 0.05$) differences in the gut content of plant, mineral, and fungal material exist between some months in each 'species' (except fungal material in artificial gut). Plant material was most numerous during autumn in artificial gut and *T. callypygos*, whereas in *O. armatus* and *O. furcifer* it was more abundant during summer, and spring respectively. Throughout most months

the plant content of artificial gut was significantly (P = 0.05) greater than in the three Collembola. Mineral material was most numerous during winter in artificial gut and *O. armatus*, and *T. callypygos* and *O. furcifer* during spring and autumn respectively. Generally, mineral content was significantly (P = 0.05) least in artificial gut and greatest in *T. callypygos*. Fungal material was most numerous in *O. armatus* and *O. furcifer* during summer, and in *T. callypygos* and artificial gut during autumn and winter respectively. Generally the fungal content of *O. armatus* was significantly (P = 0.05) the greatest of the four 'species'.

TABLE II

Mean (N = 5) percentage of plant, fungal, and mineral material in the gut contents of four 'species' of Onychiuridae during 12-months, December - November

'Species'	Gut components (%)		
	Plant	Fungal	Mineral
artificial gut	66.6	7.2	26.0
Onychiurus armatus	55.0	16.5	28.3
Onychiurus furcifer	50.7	9.8	39.4
Tullbergia callypygos	50.0	5.5	44.5
L.S.D. (P = 0.05)	2.3	2.0	2.0

Key: L.S.D. = Least significant difference between means.

On the cumulative data for the whole year the mean proportion of plant, mineral, and fungal components in each 'species' were determined (Table II) and significant (P = 0.05) differences between 'species' and components found by calculation of the least significant difference between means. The plant content of artificial gut was significantly (P = 0.05) greater than *O. furcifer*, *O. armatus*, and *T. callypygos*. The mineral content of *T. callypygos* was significantly (P = 0.05) greater than *O. furcifer*, and both these species had a significantly (P = 0.05) greater content than *O. armatus* and artificial gut. The fungal content of *O. armatus* was significantly (P = 0.05) the greatest; *O. furcifer* was significantly (P = 0.05) greater than *T. callypygos*.

DISCUSSION

The major identifiable components in the gut of *Onychiurus armatus* *Onychiurus furcifer* and *Tullbergia callypygos* were plant, fungal and mineral material. These materials were also major components in an artificial gut formed from random samples of the soil in which the above species lived. The similarity between the gut contents of the Onychiuridae and artificial gut suggests that these Collembola feed unselectively and that their gut contents

represent a random selection of the components of their environment. The data however, when subjected to statistical analysis show that significant ($P = 0.05$) differences exist between Collembola and artificial gut suggesting that Collembola were selective in their ingestion of plant, fungal and mineral material. Similarly, significant ($P = 0.05$) differences between Collembola would suggest that the three species were exploiting plant, fungal and mineral material to different degrees. There is however, no evidence to suggest that these gut components are used as food. Plant and fungal material would appear as more likely food sources than mineral particles. Mineral particles would in themselves have no obvious nutritional value. There may however be considerable nutritional value to the animal in any adhering bacteria, and organic matter.

General ecological theory suggests that species can coexist only if they occupy different ecological niches. This would lead one to expect differences of food or microhabitat between ecologically and morphologically similar species. REYNOLDSON and DAVIES (1970), in a study of food niche and coexistence in lake-dwelling triclads concluded that if two or more species of organism utilising the same limiting food resource were to coexist, without spatial or temporal separation, then food must be partitioned so that each species has at least a 30 % superiority in one area of the general food resource. In this present study, significant differences have been shown to exist for three Collembola species, between the composition of plant, fungal, and mineral material in their respective guts. These data do not however indicate a strong degree of food differentiation, or partitioning between species.

It is possible that Collembola derive nutritional requirements from materials in solution, such as the products of plant, fungal and bacterial decay. Therefore, differences may exist between species in the utilisation of food resources which are undetected by the analysis of relatively large components of the gut. Von TÖRNE (1967 a, b) has found that in certain species of Collembola, including the onychiurid, *Onychiurus cebennarius* (?) Gisin, the animal's ability to utilise certain food resources is directly related to the presence of certain bacteria because the action of bacterial enzymes makes available an otherwise unusable nutritional source. There may also be interspecies variation in the complement of digestive enzymes. ZINKLER (1968, 1971) has found differences in the activity of certain similar carbohydrases in the onychiruids, *O. armatus* and *O. subuliginatus*. These differences would enable the two different species to ingest a similar range of materials, whilst utilising different nutritional components.

CROKER (1967), in a study of niche specificity amongst a sympatric group of detritus-feeding, intertidal amphipod species, found that although the two species showed similarity in the ingested contents of their gut, the larger species ingested larger food particles than the smaller species. These two filter-feeding amphipods therefore attained a niche specificity. Comparison of the adult body length of the three Collembola in the present study shows *O. furcifer* to be larger than *O. armatus* and *T. callypygos* by approximately onethird. However, analysis of gut particle size does not indicate obvious differences between the species. Work on the feeding mechanisms of Collembola (SINGH, 1969) suggest that in those species with chewing mouthparts

(Fam. Onychiuridae, Entomobryidae, Isotomidae), plant and fungal material is obtained by tearing or scraping. The ingested particles are then ground between the mandibular molar plates prior to passing into the midgut. Therefore if any selection on the basis of particle size is made, such differences would no doubt be lost during the grinding process.

The low degree of food specificity between the three Onychiuridae may be the consequence of an excess availability of food. SLOBODKIN, SMITH and HAIRSTON (1967), however, state that there cannot be an excess of food for decomposers (such as Onychiuridae) in ecosystems, as it would cause a long term persistence of organic detritus, for which the literature provides no evidence. They further state that so-called climax plant communities exist in a highly dynamic state, continuously undergoing replacement and vertical and horizontal re-distribution of nutrients. Detritivores may therefore exist in situations in which nutrients, and consequently their own populations, fluctuate irregularly from year to year. This would imply that litter, humus, and soil may contain a mosaic of species populations in varying degrees of relationship with their environment, and that these environmental conditions may range from excess to limiting. Therefore, species at one time and place may share a resource while at another time they may actively compete.

Recent studies (e.g. JOOSSE and VELTKAMP, 1970; WITH and JOOSSE, 1971), indicate that a non-feeding phase is associated with moulting in Collembola. BÖDVARSSON (1970), and ANDERSON and HEALEY (1972) have shown that a high proportion of Collembola obtained from the field are without visible gut content. Similarly, in this present study a large proportion of individuals collected from the field were without visible gut content. The absence of visible gut content, together with evidence that a non-feeding phase may be associated with moulting, led ANDERSON and HEALEY (1972) to suggest that the average Collembola spends 40-50 % of its adult life in an inactive or semi-active condition in which it does not feed. If about half the adult population is in a non-feeding phase at any one time intraspecies competition for food may be reduced and food for further individuals or species may be made available.

Undetected differences in microhabitat may exist between the species. As suggested by FREEMAN (1968) and MILLER (1969) a horizontal layer of the soil profile may contain many 'compartments' each with a similar range of resources, but between which movement is restricted, so that a mosaic of microhabitats and species are present.

HUTCHINSON (1951) states that 'fugitive' species (species which become extinct in one locality as they succumb to competition, but survive by reestablishing themselves in another locality as a new niche opens) may coexist in a niche with more successfully competitive species and compete for the same resources until the dominant species eliminates the less successful competitor. In this present study *O. armatus* was most numerous of the three Collembola. *O. furcifer* and *T. callypygos* may therefore be 'fugitive' species coexisting with *O. armatus* and sharing similar food resources.

The reason for the low degree of food specificity amongst the species in this study is uncertain. The technique employed, or one or more of the discussed factors may be responsible for this apparent lack of specificity.

It is apparent from the present study that gut analyses may provide a useful line of investigation in an understanding of the trophic interrelationships of the soil fauna.

Acknowledgements

I am grateful to Professor D. R. Arthur and the late Dr I. N. Healey of the Department of Zoology, King's College, University of London, England, for laboratory facilities and equipment. This research was conducted during the tenure of a National Research Fellowship, awarded by New Zealand Department of Scientific and Industrial Research.

Summary

The gut contents of populations of *Onychiurus armatus, O. furcifer,* and *Tullbergia callypygos,* inhabiting soil from the nest of a woodland ant (*Formica rufa* L.), together with the gut content of a hypothetical Collembola, were studied during 12-months.

Significant ($P = 0.05$) month to month and seasonal variations in the proportions of the major gut components; plant, fungal, and mineral material, were generally found in all four ' species '.

Significant ($P. = 0.05$) differences exist between Collembola and artificial gut, and between Collembola species, which would suggest that Collembola were selective in their ingestion of plant, fungal, and mineral material. Thesa data do not however, show the strong degree of food differentiation which would be expected between sympatric species. The possibilities are discussed of subtle microhabitat differences between these species, or differences of feeding that cannot be demonstrated by gut contents analysis, such as differences in gut enzyme compliment leading to selective absorption from the gut contents.

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